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INFLORESCENCE ARCHITECTURE AND FLORAL MORPHOLOGY OF *ARATITIYOPEA LOPEZII* (XYRIDACEAE)

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ABSTRACT

Aratitiyopea lopezii is a robust perennial species of Xyridaceae from seasonally saturated, mid- to high-elevation, sandstone and granite sites in northern South America. The species lacks the scapose inflorescence characteristic of Xyridaceae and, having the gestalt of a rhizomatous bromeliad, it is seemingly aberrant in the family. However, closer examination confirms features consistent with the family and the previously noted morphological similarities to *Orectanthe.* Details of inflorescence structure and floral morphology are presented and compared to other genera of Xyridaceae.

Key words: *Aratitiyopea,* Bromeliaceae, gynoecium appendage, inflorescence, *Navia,* nectary, *Orectanthe,* osmophore, pollen, Xyridaceae.

INTRODUCTION

Aratitiyopea (Xyridaceae) is a monospecific genus of herbaceous perennial plants with long, decumbent stems that terminate in a congested inflorescence (Fig. 1). Isolated populations occur in semideciduous forests in areas of high annual precipitation (2800–4000 mm, Campbell 2004*a*) that are located on ancient sandstone and granite in the Guayana region of northern South America and on the geologically similar, although younger (Foster and Beltran 1997), Cordillera del Cóndor in northern Peru. The habit and escapose inflorescence, with large flowers and colorful bracts, is strikingly different from species in the more familiar genera *Xyris* and *Abolboda.* Indeed, *Aratitiyopea lopezii* (L. B. Sm.) Steyerm. & P. E. Berry was originally ascribed to *Navia* Schult. f., a moderate-sized genus of Bromeliaceae endemic to the Guayana region (Holst and Luther 2004). Interestingly, the features of this species that were unique for *Navia*—the flower size and magenta corolla (Smith 1951)—are also unusual for Xyridaceae. The morphology and possible systematic affinities of the species remained obscure until additional material from an expedition to Cerro Aratitiyope (Amazonas State, Venezuela) was examined; the authors concluded that the uniseriate androecium and appendages on the ovary were consistent with Xyridaceae (Steyermark and Berry 1984). They remarked on the similarity to *Orectanthe ptaritepuiana* (Steyerm.) Maguire, a little-known species with stems that trail over high elevation scrub vegetation.

Xyridaceae are included in the broadly defined Poales, part of the large commelinid clade (Chase et al. 2000; Soltis et al. 2000; Angiosperm Phylogeny Group II [APG II] 2003). The family is usually considered closely related to Eriocaulaceae (Cronquist 1981; Dahlgren et al. 1985; Stevenson and Loconte 1995; Thorne 2000) and was included in Dahlgren et al.'s (1985) petaloid Commelinales. As presently understood, Xyridaceae include the widespread genus *Xyris* (ca. 360 spp.), and four genera endemic to northern South America: *Abolboda* (22 spp.), *Achlyphila* (1 sp.), *Aratitiyopea* (1 sp.), and *Orectanthe* (2 spp.) (Campbell 2004*b*). Xyridaceae are characterized by a scapose spike inflorescence, and the few exceptions to this growth form (i.e., some *Abolboda* species, *Achlyphila,* and *Aratitiyopea*) have not been critically evaluated. In the taxonomic literature, the inflorescence of *Aratitiyopea* is described as a bracteate hemispheric capitulum (Steyermark and Berry 1984; Kral 1992, 1998) of fascicles "... *in foliorum centro nidulans* ..." (Smith 1951). While the inflorescence structure is largely uniform in Xyridaceae, it has long been noted that floral morphology is heterogeneous (Maguire and Wurdack 1960; Dahlgren et al. 1985; Rudall and Sajo 1999; Table 1). The purpose of this contribution is to further describe the floral morphology and clarify the inflorescence architecture of *Aratitiyopea lopezii.*

MATERIALS AND METHODS

Specimens of *Aratitiyopea* from the following herbaria have been studied: COL, F, GH, K, MO, NY, SEL, US, and VEN. Living samples were fixed in formalin-propionic acid-alcohol (1 : 1 : 18 v/v, FPA), and transferred to 70% ethanol (*Campbell et al. 734, 766, 813* [NY, TFAV, VEN]). Sectioned material was embedded in Paraplast® Plus (Oxford Labware, St. Louis, Missouri, USA) using standard procedures, sectioned with a rotary microtome, and stained with safranin and astra blue. For scanning electron microscopy, flower buds were dissected in 70% ethanol, dehydrated in a series to 100% acetone and critical point dried; pollen grains were dissected from ethanol preserved flowers, and air dried on stubs. All samples were coated with gold palladium in a Hummer 6.2 sputtering system and viewed with a JEOL JSM-5410LV scanning electron microscope.

OBSERVATIONS AND DISCUSSION

Inflorescence Architecture

As mentioned above, the inflorescence of most Xyridaceae (98% of the species) is a globose to turbinate, or capitulate spike, borne on a scape. Escapose inflorescences are found in two diminutive *Abolboda* species that have reduced inflorescences. In many other *Abolboda* species one or more pairs of subopposite bracts occur along the scape, and a few

Fig. 1.—A flowering plant of *Aratitiyopea lopezii.*

of these species bear compound inflorescences of reduced spikelets. The inflorescence of *Achlyphila disticha* Maguire & Wurdack is also compound, scapose, and with a reduced number of relatively long-pedicellate flowers per branch.

The reproductive system of *Aratitiyopea* terminates the vegetative axis as a double raceme of 6–16 racemes (Fig. 2). Occasionally the main axis of the inflorescence also bears a fully developed green leaf. The individual racemes are short-pedunculate, subtended by a foliose bract, and bear a bicarinate adaxial prophyll (Fig. 2). These racemes are formed by several to many flowers in a 3/8 phyllotactic spiral. This suite of inflorescence features (a compound inflorescence, with many-flowered branches, not borne on a scape) is not known in other Xyridaceae.

Flower Structure

Typical of Xyridaceae, the flowers of *Aratitiyopea* open in the early morning and remain open for several hours. A striking feature of *Aratitiyopea lopezii* is the robustness of the plants, and the concomitant large flowers (ca. 6.5 cm) relative to most Xyridaceae. Flowers are composed of four whorls (Fig. 3) and subtended by a foliose, persistent magenta bract. Two color morphs have been collected thus far, and in at least the one population studied, they are sympatric, and flower simultaneously. Plants bear flowers with either a white corolla and stigma, or a magenta corolla and stigma (but a white style and filaments).

Perianth.—The Xyridaceae perianth is trimerous and bicyclic, with a distinct calyx and corolla. Variation occurs in the form, and persistence of the median (abaxial) sepal, and fusion of the corolla (Table 1). In *Aratitiyopea* the median sepal is subequal to the lateral sepals (Fig. 4A), and all are persistent in fruit. The sepals contain numerous vascular bundles. The corolla is fused into a long (5.5 cm) tube, and unique to Xyridaceae, the free petal limbs are contorted (Fig. 5). Within the parenchymatous ground tissue of each petal there are numerous more-or-less equally sized, evenly distributed, vascular bundles, and a central larger bundle from which the epipetalous stamen trace diverges. The petals are delicate, but lack the fimbriate apex typical in the family. A calyx of subequal, persistent sepals is also found in the genus

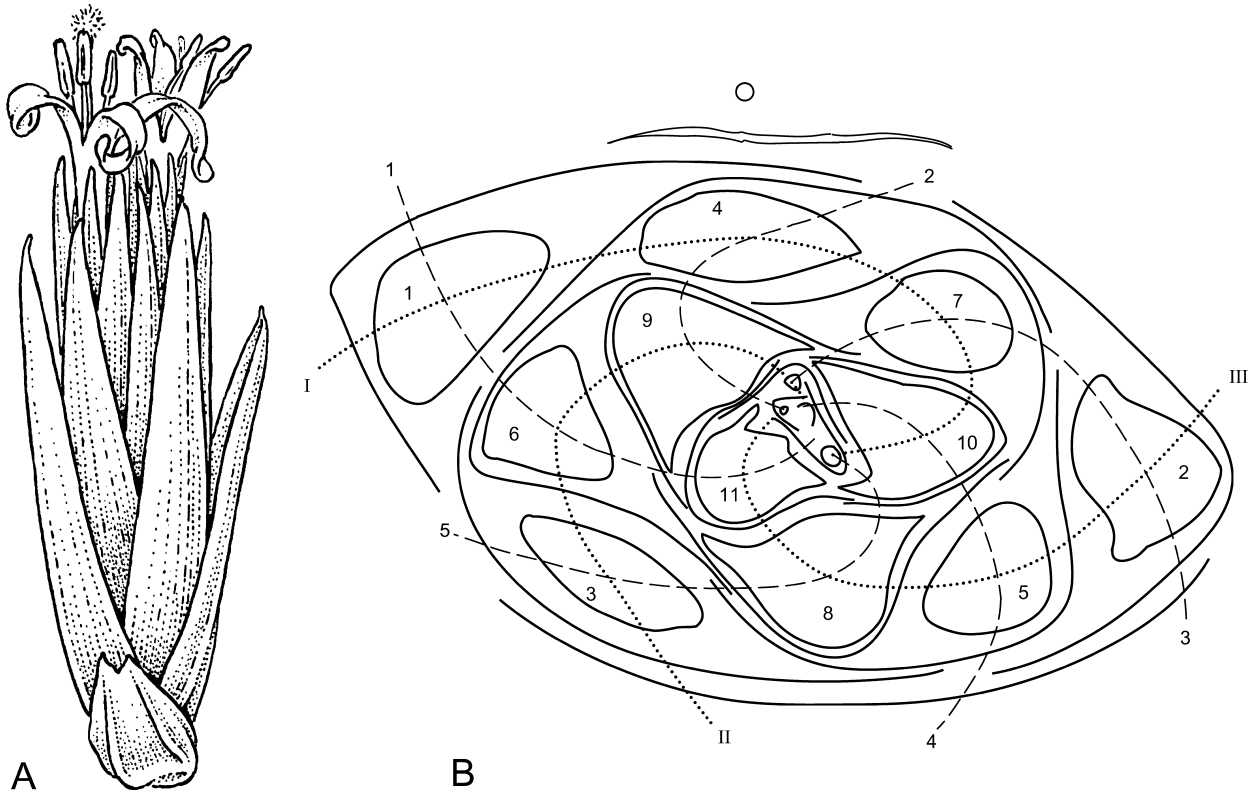

Fig. 2.—*Aratitiyopea lopezii.*—A. An inflorescence branch, with an adaxial prophyll.—B. Cross section through the base of the raceme, and parastiches of the phyllotactic spiral (note the orientation is reversed from A). (A drawn by Bobbi Angell).

Table 1. Floral characteristics of the genera of Xyridaceae.

Genus	Sepals	Corolla	Staminodia	Stamens	Pollen	Gynoecium	Ovules
Abolboda Humb. & Bonpl.	2 or 3, then dimorphic if 3, median fugacious	sympetalous, salverform or porrect blue, purple, white, poly-, sometimes monosymmetric	present or absent, filamentous	ventrifixed, dehiscence extrorse	spherical, inaperturate	trilocular, ovary usually 3-appendaged, appendages polymorphic, style solid or hollow, stigma branched	anatropous
Achlyphila Maguire & Wurdack	3, subequal, all persistent	choripetalous, funnelform, yellow, polysymmetric	absent	ventrifixed, dehiscence latrorse	spherical, inaperturate	trilocular, style?, stigma capitate	anatropous?
Aratitiyopea Steyerm. & P. E. Berry	3, subequal, all persistent	sympetalous, salverform, white or magenta, polysymmetric	absent	basifixed, dehiscence latrorse	spherical, inaperturate	trilocular, ovary 3-appendaged, appendages monomorphic, style solid, stigma branched	anatropous
Orectanthe Maguire	3, dimorphic, median caducous	Sympetalous, porrect, yellow, monosymmetric	absent	basifixed, dehiscence introrse	spherical inaperturate	trilocular, ovary 3-appendaged, appendages monomorphic, style solid, stigma branched	anatropous
Xyris L.	3, dimorphic, median fugacious	chori- or sympetalous, tubular, yellow, poly-, occasionally monosymmetric	rarely absent, usually elaborate, usually distally adnate to adjacent petals	basifixed, dehiscence latrorse or extrorse	elongate, sulcate	uni- or trilocular, style hollow stylodia or stigma branched	orthotropous

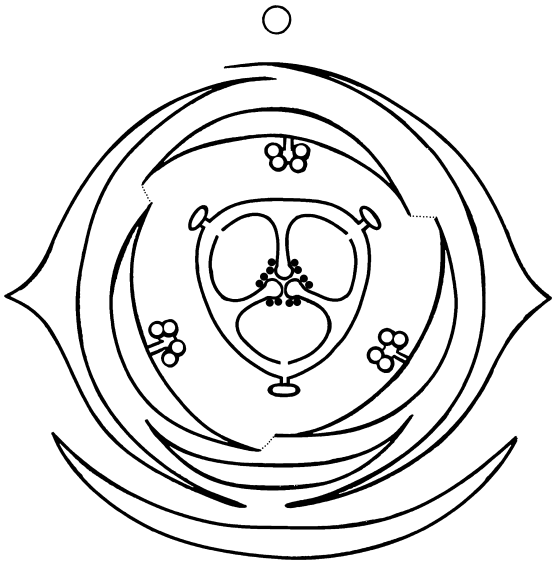

Fig. 3.—Floral diagram of *Aratitiyopea.* The large dorsal gynoecial appendages are depicted; dorsal stigma lobes not shown.

Achlyphila, which occurs at high elevations, whereas in the other genera the sepals are strongly dimorphic and fugacious (*Abolboda* and *Xyris*) or caducous (*Orectanthe*). Fused corollas are present in all of the genera except *Achlyphila.*

Androecium.—The form of the stamens and presence of an inner androecial whorl, expressed solely as staminodia, vary in the family. The anthers are hypogenous or epipetalous, basifixed or ventrifixed, tetrasporangiate, with longitudinal dehiscence that is either extrorse, latrorse, or introrse. In *Aratitiyopea,* the androecium is uniseriate with three antepetalous fertile stamens. The filaments are epipetalous, and supplied by a single vascular trace from the petal midvein (Fig. 4C). The anthers are basifixed, dehisce latrorsely, and the connective projects slightly beyond the thecae. The yellow pollen grains are large (to 180 μm), inaperturate, with a dense surface ornamentation of very large bacula interspersed in a matrix of smaller ones (Fig. 6). Anthers of *Orectanthe* are also basifixed, and have a slight connective protrusion, whereas in other Xyridaceae the connective is sunken. Inaperturate pollen occurs in *Achlyphila, Abolboda,* and *Orectanthe*; pollen of the latter two have surface ornamentation similar to *Aratitiyopea.* Antesepalous staminodia occur in some *Abolboda* species and are delicate and filamentous; those of *Xyris* are well-developed structures, forming a conspicuous part of the floral display.

Gynoecium.—In all Xyridaceae, the gynoecium is tricarpellate and the ovary superior. In *Aratitiyopea,* the ovary is trilocular with numerous biseriate, anatropous ovules (Fig. 7) borne on intruded placentae (Fig. 4A). The style contains a solid column of transmitting tissue (Fig. 4C), and branches distally into three stigmatic lobes that are further ramified into a plumose stigma (Fig. 8). A large, fleshy gland, or appendage, develops on the dorsal flank of the carpel (Fig. 9). At anthesis the stalked appendage is atop the ovary, and the distal, reflexed massive portion occupies most of the diameter of the floral tube (Fig. 4B). In this region, the numerous vascular bundles are mostly composed of phloem,

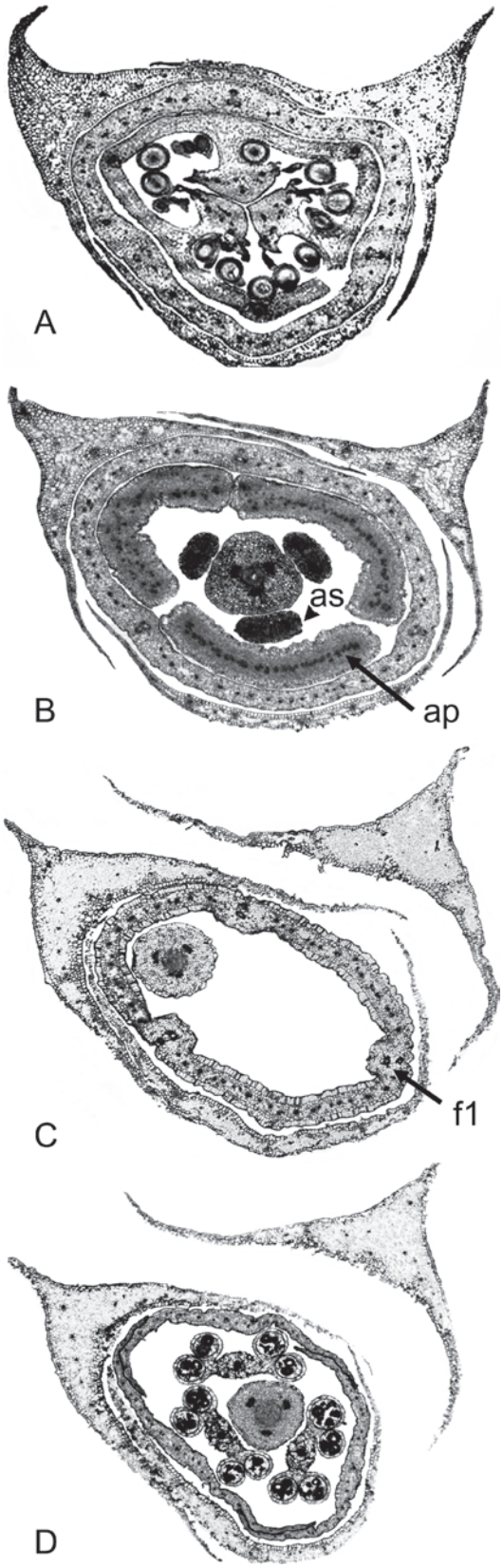

Fig. 4.—Acropetal sections through a flower of *Aratitiyopea lopezii.*—A. Mid-ovary, showing intruded placentae.—B. Near the ovary apex, showing the appendages (ap = distal portion of the appendage, abaxial carpel; as = stalk of the same appendage).—C. Divergence of the staminal filaments (f1 = filament 1).—D. At the level of the anthers.

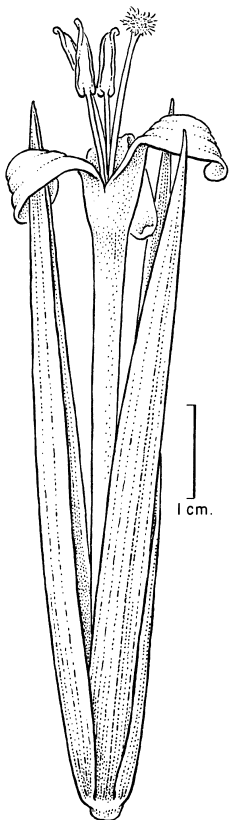

Fig. 5.—*Aratitiyopea lopezii.* Abaxial view of a flower at anthesis. (Drawn by Bobbi Angell).

and cells of the ground tissue are densely cytoplasmic with large nuclei. Near the periphery, the tissue becomes aerenchymatous. In contrast to the regularly shaped cells of the epidermis along the appendage stalk, in the distal portion the cells form a glandular, papillate epithelium that lacks stomata (Fig. 4D, 10).

A trilocular ovary with intruded placentae is common, but not uniform, within the family, and is usually described as axile placentation. *Orectanthe* and some *Abolboda* species

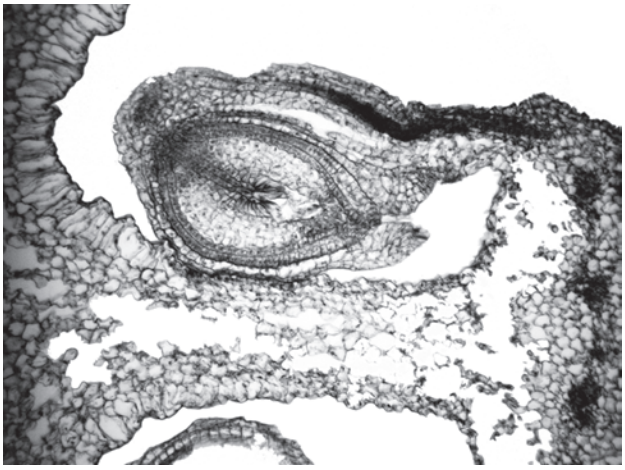

Fig. 7.—Ovule of *Aratitiyopea lopezii.*

have solid styles, an uncommon condition in monocotyledons (see Rudall et al. 2002), whereas the style is hollow in other *Abolboda* and *Xyris* (but unknown in *Xyris* sect. *Pomatoxyris* Endl. and in *Achlyphila*). The gynoecium of *Achlyphila* is incompletely known with respect to the surface of the stigma, and fusion of the carpels within the ovary and through the style. While it appears to lack appendages (Maguire and Wurdack 1960; Kral 1998), it should be noted that the delicate appendages in *Abolboda* are sometimes impossible to detect, especially in rehydrated flowers (Kral 1992, pers. obs.).

Gynoecium appendages are large and similarly positioned in *Orectanthe,* and are reduced, unequal, and occur along the style in *Abolboda.* While the tissue of appendages in *Aratitiyopea* is clearly of a secretory type, their physiological function has yet to be determined. A close relationship to Eriocaulaceae, with nectar-secreting gynoecial appendages (Stützel 1984; Rosa and Scatena 2003; see also Tiemann 1985), would lead one to predict that the glands in Xyridaceae have the same function. However, no nectar has been detected in the floral tubes of *Aratitiyopea,* and while glands with a large phloem content is associated with secre-

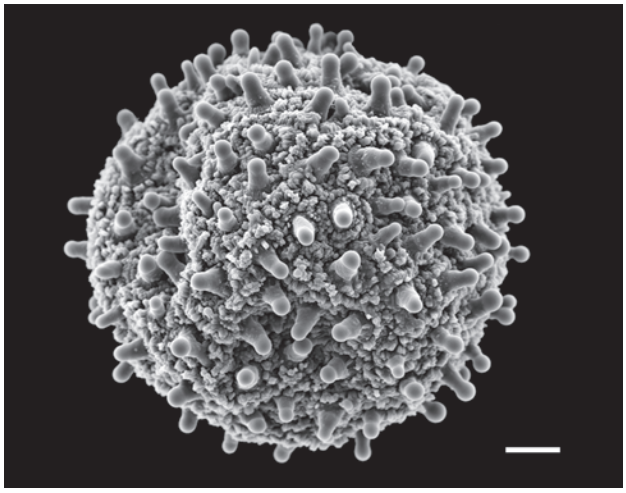

Fig. 6.—Pollen grain from *Aratitiyopea lopezii.* (Scale bar = 5 μm).

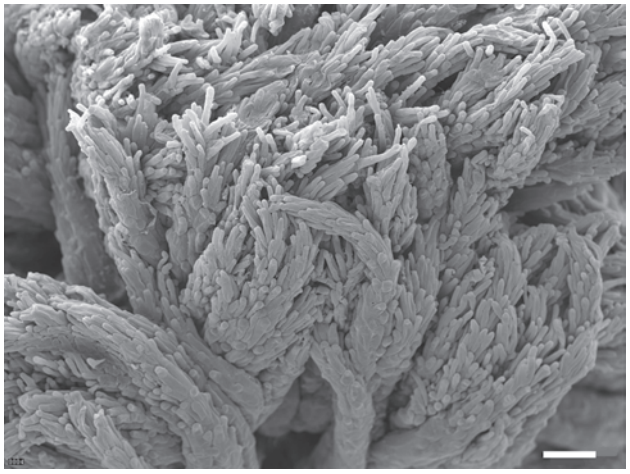

Fig. 8.—Plumose stigma of *Aratitiyopea lopezii.* (Scale bar = 100 μm).

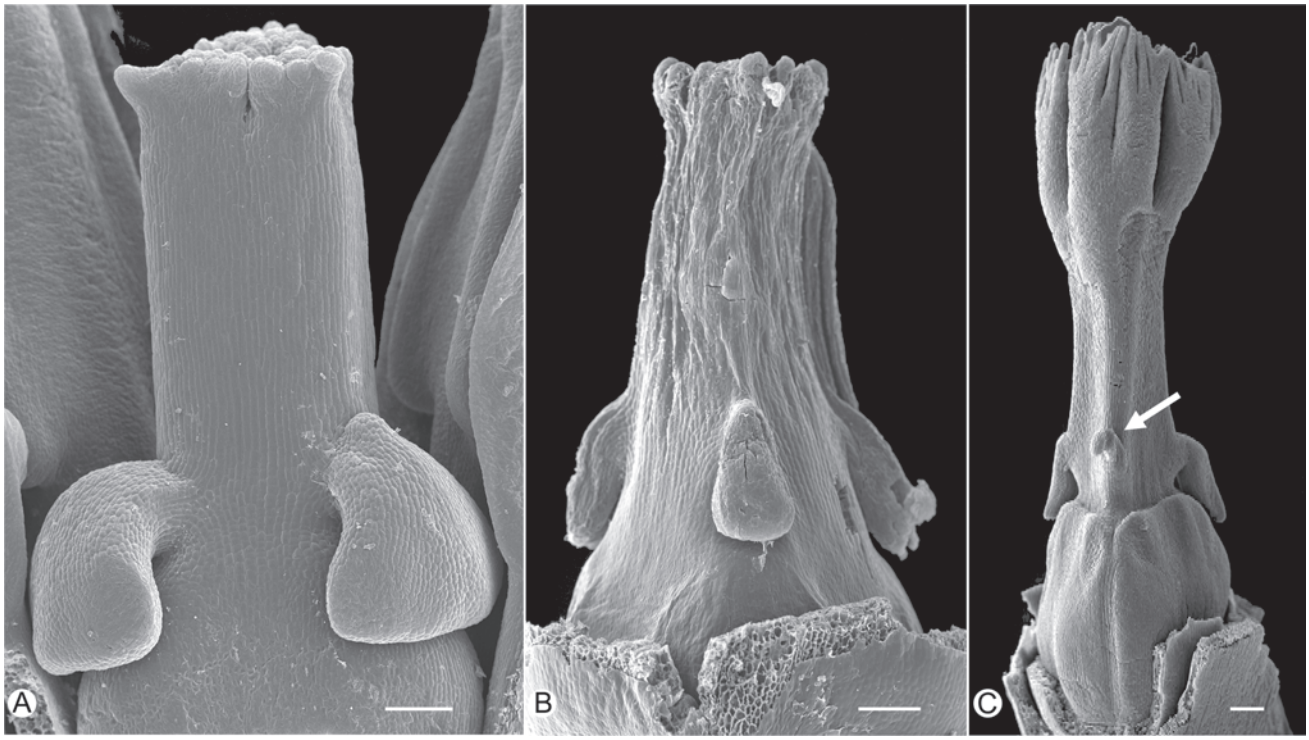

Fig. 9.—Immature gynoecia of—A. *Aratitiyoea lopezii,* adaxial view.—B. *Orectanthe sceptrum* (Oliv. ex Thurn) Maguire, abaxial view (*Campbell et al. 745*).—C. *Abolboda grandis* Griseb., abaxial view, arrow: reduced appendage (*Campbell et al. 625*). (All scale bars 100 μm).

tion of dilute nectar (Esau 1965), it is also found in osmophores (Vogel 1990).

CONCLUSIONS

Aratitiyopea is an unusual Xyridaceae with features such as a trailing habit, long, broad leaves, and a prolific compound inflorescence of large flowers, that are probably adaptations to the habitat it occupies. While the majority of Xyridaceae occur in open-canopied habitats including savannas, rocky outcrops, and bogs, *Aratitiyopea* is found under dense-canopied forest in scrub vegetation and on sheer rock faces, habitats shared with many Bromeliaceae.

Structurally, *Aratitiyopea* is most similar to *Orectanthe,* and the two share with *Abolboda* a fused corolla, an appendaged gynoecium with intruded placentae and a solid style, and inaperturate pollen with conspicuous ornamentation (Table 1). The monophylesis of Xyridaceae is still in debate (see APG II 2003; Michelangeli et al. 2003; Davis et al. 2004), with *Abolboda, Aratitiyopea,* and *Orectanthe* often

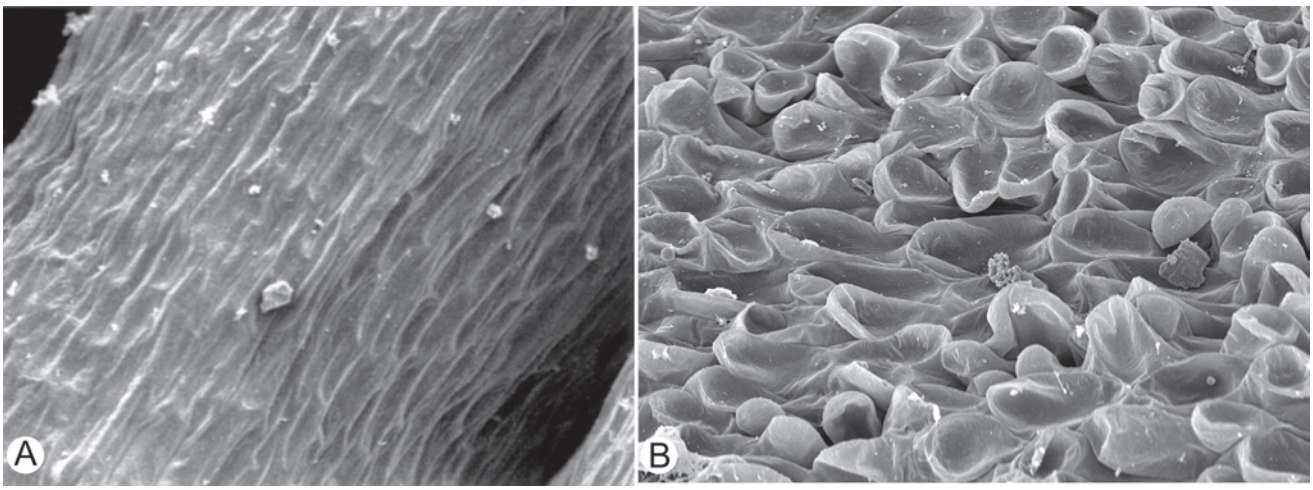

Fig. 10.—Scanning electron micrograph of the surface of a gynoecium appendage of *Aratitiyopea lopezii.*—A. Epidermis near the basal stalk portion.—B. Epidermis modified as epithelium from the distal region.

forming a clade independent of *Xyris.* A satisfying resolution of relationship based on morphological synapomorphies awaits pending studies of *Achlyphila,* which presents an interesting combination of features shared by *Abolboda, Aratitiyopea,* and *Orectanthe* on the one hand (e.g., a uniseriate androecium and inaperturate pollen) and *Xyris* on the other (e.g., unifacial leaves, and free, yellow petals; Table 1).

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